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Population structure of herring *(Clupea pallasi)* in British Columbia: an analysis using microsatellite loci

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Abstract

The purpose of this study was to determine population structure of herring (*Clupea pallasi*) in British Columbia. Variation at 15 microsatellite loci (Cpa4, Cpa6, Cpa8, Cpa27, Cha63, Cpa100, Cpa103, Cpa104, Cpa107, Cpa107a, Cha113, Cpa114, Cpa115, Cpa125, Cpa134) was surveyed in approximately 11,000 herring from 65 sampling locations. F_{ST} estimates by locus varied between 0.0005 and 0.0073, with the mean over all loci of 0.0023. Other than for herring spawning in Skidegate Inlet, there was no evidence of substructure for herring along the east coast of the Queen Charlotte Islands. In the Strait of Georgia, there was no evidence of substructure within the stock except possibly for herring spawning in Secret Cove along the mainland coast and Esquimault Harbour (Portage Inlet) at Victoria. Strait of Georgia herring were distinct from those spawning at Cherry Point in Puget Sound, Washington. No evidence of substructure was observed in the west coast of Vancouver Island stock, although herring spawning in Winter Harbour may be distinct from those spawning further south along the coast. No evidence of substructure was observed in either the North Coast or Central Coast stocks. Annual variation in allele frequencies within the five stocks of herring in British Columbia defined for assessment and management was larger than any differences among stocks, and thus, on average, there is no genetic differentiation among the five defined stocks. The lack of genetic differentiation among herring stocks in British Columbia is consistent with straying rates among stocks that is sufficient to homogenize allele frequencies over broad areas. Herring spawning in southeast Alaska may be distinct from those spawning further south on the Queen Charlotte Islands and in the north coast of British Columbia. For locations where genetically distinct populations occur, differences in timing of spawning are the main isolating mechanisms, although geographic isolation of the spawning population may also have some effect in maintaining genetic distinctiveness of the spawning population.

Résumé

L'étude a pour but de déterminer la structure de la population de hareng (*Clupea pallasi*) en Colombie-Britannique. Une variation a été relevée à 15 locus de microsatellites (Cpa4, Cpa6, Cpa8, Cpa27, Cha63, Cpa100, Cpa103, Cpa104, Cpa107, Cpa107a, Cha113, Cpa114, Cpa115, Cpa125, Cpa134) chez environ 11 000 harengs provenant de 65 lieux d'échantillonnage. Les estimations de F_{ST} par locus ont varié entre 0,0005 et 0,0073, la moyenne pour tous les locus étant de 0,0023. À part des harengs frayant dans Skidegate Inlet, rien ne démontrait l'existence d'une structure secondaire dans le cas du hareng le long de la côte est des îles de la Reine Charlotte. Dans le détroit de Georgia, il n'y avait pas de signe de structure secondaire dans le stock, à l'exception peut-être de harengs frayant à Secret Cove le long de la côte continentale et à Esquimault Harbour (Portage Inlet) à Victoria. Le hareng du détroit de Georgia se distinguait du hareng frayant à Cherry Point dans Puget Sound (État de Washington). Aucun signe de structure secondaire n'a été décelé dans le stock de la côte ouest de l'île de Vancouver, bien que les harengs frayant à Winter Harbour peuvent être distincts de ceux frayant plus au sud le long de la côte. Aucun indice de structure secondaire n'a été décelé dans l'un ou l'autre des stocks du nord et du centre de la côte. La variation annuelle dans les fréquences des allèles dans les cinq stocks de hareng de la Colombie-Britannique définis pour l'évaluation et la gestion était plus importante que toute différence entre les stocks; ainsi, en moyenne, il n'y a pas de différenciation génétique entre les cinq stocks définis. L'absence de différenciation génétique entre les stocks de hareng en Colombie-Britannique est cohérente avec le taux de vagabondage entre les stocks qui est suffisant pour homogénéiser les fréquences des allèles sur de vastes superficies. Les harengs frayant dans le sud-est de l'Alaska sont peut-être distincts de ceux frayant plus au sud sur les îles de la Reine Charlotte et dans le nord de la côte de la Colombie Britannique. Là où les populations sont génétiquement distinctes, des périodes de fraye différentes constituent les principaux mécanismes d'isolement, quoique l'isolement géographique de la population de reproducteurs puisse aussi contribuer d'une certaine manière à maintenir sa distinction génétique.

Introduction

Delineation of population structure is fundamental to the assessment, conservation, and management of herring. Population structure of herring in British Columbia has been investigated with a variety of techniques. Early work centered on tagging (reviewed by Hay et al. 1999), with about 84% of herring returning to spawn in the region in which they were tagged (Hourston 1982). Spawning time and location were also thought to be important factors in delineating population structure (Haegele and Schweigert 1985). In British Columbia, herring are currently managed on the basis of the existence of five discrete stocks (Schweigert, 2000). The main stocks are defined as the Strait of Georgia, west coast of Vancouver Island, the Central Coast, the North Coast, and the southeast coast of the Queen Charlotte Islands. However, local population structure has been a particularly contentious issue raised in the management of herring in British Columbia, with some thought that there are unique substocks or populations within these five stocks, perhaps at the level of bays or inlets.

The level of reproductive isolation, if any, among subcomponents or local populations, is uncertain. If there are discrete genetic stocks, then genetic differences should be observable among stocks, repeatable over time, and individual fish should return to spawn in the same geographic area from which they originated. Genetic differentiation at neutral genetic loci among spawning groups, indicative of restricted gene flow and independent population dynamics among the groups, is a good indicator of population structure. Moreover, if sufficient genetic differentiation is observed among populations, the genetic markers can be used to provide estimates of population or stock composition in areas of population mixing. This enables determination of catch by population with subsequent estimation of exploitation rates, allowing managers to protect less productive populations from overexploitation in regions of mixing.

Fidelity of spawning individuals to specific areas, with little exchange of spawners among areas, is a basic requirement in the designation of a "stock". The restriction of gene flow among spawning groups that results from this fidelity enables the development over time of genetic differentiation. For a marine fish such as herring, a stock may consist of a single large, randomly-breeding aggregate, or may be subdivided into smaller groups within which mating is random, but among which there is more limited exchange of individuals. These local populations within a stock are more similar to each other than to populations in another stock complex. Analysis of genetic variation provides definitive analysis of whether or not there is restricted gene flow among putative populations and whether or not the putative populations constitute genetically distinct spawning populations. It is obviously important that the screening techniques used are able to detect genetic differentiation among putative populations should such differentiation exist. Previous analyses of genetic variation in eastern Pacific herring, as determined from allozyme variation, indicated that genetic differentiation was observed only over relatively large geographic areas, such as between herring from Asian and eastern Pacific regions, and perhaps within the eastern Pacific between Gulf of Alaska and more southern areas (Grant and Utter 1984). In the western Pacific Ocean, differentiation at allozymes indicated that genetic differentiation could occur on a more localized basis (Kobayashi et al. 1990), similar to the local differentiation observed in Atlantic herring (Jorstad et al. 1994; Turan et al. 1998). In a survey of mitochondrial DNA variation, local differentiation was not observed in eastern Pacific herring (Schweigert and Withler 1990), nor was any observed in ribosomal DNA sequence variation (Domanico et al. 1996). Analysis of variation at microsatellite DNA loci suggested that differentiation was detected among populations in more local areas of the eastern Pacific Ocean than with previous techniques for genetic analyses (O'Connell et al

1998), with similar results observed in Atlantic herring (Shaw et al. 1999). Shaw et al. (1999) suggested that microsatellites uncover genetic structuring in populations that allozymes and mtDNA studies do not detect.

The primary objective of this study was to use microsatellite variation to investigate population structure of herring in British Columbia, in particular within the five defined stocks for management. We examined whether there are distinct "bay or inlet populations" of herring, i.e., is there genetic differentiation among herring populations in neighboring bays or inlets within currently managed stocks in British Columbia or are the currently defined stocks homogeneous genetic populations? The level of differentiation among the five defined stocks in British Columbia was also evaluated.

Materials and Methods

Collection of baseline DNA samples and laboratory analysis

Samples were obtained from adult herring immediately prior to, or at, or immediately after spawning during March to May of each year. The only exception was a juvenile sample collected in early June in Bute Inlet which was used to characterize herring from the area. Samples were collected from 59 locations in British Columbia, five in southeast Alaska, and one in Washington, with approximately 11,000 herring scored at 15 microsatellite loci (Table 1). Samples were generally obtained by a crewed vessel equipped with either a gillnet or purse seine that conducted testfishing at a particular location, and were usually collected during March in the year of spawning. The Portage Inlet sample was collected from sport-caught herring in Victoria harbour. Genomic DNA was extracted using the chelex resin protocol of Small et al. (1998) from operculum punches from herring sampled between 1997 and 2000 and preserved in 90% ethanol. PCR products at 13 microsatellite loci: *Cha63*, *Cha113* (O'Connell et al. 1998), *Cpa6, Cpa27, Cpa100, Cpa104, Cpa107, Cpa115, Cpa125, Cpa134* (Miller et al. 2001), and *Cpa103*, *Cpa107a*, and *Cpa114* (Olsen et al. pers. comm.) were size fractionated on denaturing polyacrylamide gels and allele sizes determined with the ABI 377 automated DNA sequencer and Genescan software. PCR products at two microsatellite loci (*Cpa4, Cpa8*) (Miller et al. 2001) were size fractionated on non-denaturing polyacrylamide gels by staining with 0.5 mg/ml ethidium bromide in water and illuminating with ultraviolet light. Nelson et al. (1998) provided a more complete description of gel electrophoretic conditions. Three 20-bp marker lanes were run on each gel, with the size of the amplified alleles determined from the molecular size grid created with the 20-bp markers. Beacham and Wood (1999) provided a more complete description of the methods used to identify alleles using this technology.

Data Analysis

Each population at each locus was tested for departure from Hardy-Weinberg equilibrium using the Genetic Data Analysis (GDA) software (Lewis and Zaykin 2001). Tests of genetic differentiation utilizing pairwise comparisons among samples were conducted using GENEPOP (Raymond and Rousset 1995) with the Markov-chain approach using χ^2 probability values. The dememorization number was set at 1,000, and 50 batches were run for each test with 1,000 iterations/batch. Critical significance levels for simultaneous tests were evaluated using sequential Bonferroni adjustment (Rice, 1989). F_{ST} estimates for each locus were calculated with GDA, and the standard deviation of the estimate for an individual locus was determined by jackknifing over samples and for all loci combined by bootstrapping over loci. F_{ST} (or the coancestry coefficient) is the correlation of genes of different individuals in the same population and can range from 0 to 1. The formula is: $F_{ST} = \delta_p^2/[p(1-p)]$ where δ_p^2 is the variance over

samples in the frequency of allele A, and p is the average sample frequency of allele A. Cavalli-Sforza and Edwards (1967) chord distance (CSE) was used to estimate distance among samples, with a neighbor-joining dendrogram generated with PHYLIP (Felsenstein 1993).

Hierarchical analyses of allele frequency variation with stocks were conducted with GDA using a nested random effects model. Variance components of population differences and annual variation within populations were determined for each of the five managed stocks of herring in British Columbia. Negative variance components were set to zero in the relative diversity analysis. As samples were derived from a number of sites in British Columbia, putative populations were defined within each stock. For the east coast of the Queen Charlotte Islands, the Selwyn Inlet samples were defined as a single putative population, as well as the Section Cove and Skaat Harbour samples, and also the Skincuttle Inlet samples. Skidegate Inlet samples were also considered as a separate population. For the Strait of Georgia stock, three putative populations were defined along the east coast of Vancouver Island. These consisted of samples taken near Denman and Hornby Islands (Longbeak Point, Henry Bay , Norman Point , Whalebone Point, Bowser, Chrome Island, Komas Bluff , and Fanny Bay), near Parksville (French Creek and Parksville Bay), and near Nanaimo (Jessie Island, Hammond Bay, and Link Island). For the west coast of Vancouver Island, four putative populations were defined. These were near Barkley Sound (Spilling Islet, Castle Rock , Bryant Islands, and Forbes Island), in Sydney Inlet (samples collected in 1999 and 2000), in Nootka Sound (Nootka Sound, McKay Pass, and Hesquiat Harbour), and Esperanza Inlet (1999, 2000 samples). Two putative populations were defined for the North Coast, one north of Prince Rupert (Big Bay, Venn Passage, and Tree Bluff) and one southwest (Gurd Island, Kitkatla Channel). Four putative populations were defined for the Central Coast, one near Swindle Island (East Higgins, Kitasu Bay), one near Bella Bella (Spiller Channel, Powell Anchorage, Dundivan Inlet, Stryker Bay, and Gale Passage), one near Rivers Inlet (Illahie Inlet, Pruth Anchorage), and one near Smith Inlet (Takush Harbour, Smith Inlet). Population structure of herring sampled near Johnstone Strait was also evaluated, with putative populations defined near Port Hardy (Hardy Bay, Beaver Harbour), Thompson Sound (1997, 1999), Loughborough Inlet (1997, 1999), and Bute Inlet (1999 sample split into two equal parts for analysis).

Hierarchical analyses of allele frequency variation was conducted among the five managed stocks of herring in British Columbia. As little differentation was observed among putative populations within stocks, all samples collected in a year were pooled for each stock. Skidegate Inlet samples were not included in the east coast of the Queen Charlotte Islands stock as the population was distinct and it was outside of the management area. The Secret Cove and Portage Inlet samples were not included in the Strait of Georgia stock as they may be distinct populations. The Winter Harbour sample was not included in the west coast of Vancouver Island stock as it may be distinct and it was outside of the management area. Three years of samples were available for analysis for the east coast of Queen Charlottes Islands stock (1998, 1999, 2000) and the Strait of Georgia, west coast of Vancouver Island, and Central Coast stocks (1997, 1999, 2000), but only two years of samples were available for the North Coast stock (1999, 2000). When a putative Johnstone Strait stock was included in the analysis, three years of samples were available (1997, 1999, 2000).

Results

Variation within stocks

All microsatellite loci surveyed were highly polymorphic, with the number of alleles per locus ranging from 24 at Cpa4 to 63 at Cpa104, with an average of 39 alleles per locus (Table 2). Expected heterozygosity estimates were very similar among sampling sites, ranging from 0.84 to 0.90 (Table 1). Genotypic frequencies at each locus within sampling sites generally conformed to Hardy-Weinberg equilibrium (HWE) expectations, with the exception of Cpa115 and Cpa8. At Cpa115, over 50% of the sampling sites were not in HWE, and at Cpa8, approximately 10% of the sampling sites were not in HWE. One or more nonamplifying allele(s) was likely present at these loci, or unequal amplification of alleles may have resulted in the failure to detect large alleles in some heterozygous individuals. The mean F_{ST} value over 65 samples and 15 loci surveyed was 0.0023 (0.0021 with Cpa8 and Cpa115 excluded), with significant single-locus values observed at 13 loci (Table 2).

Population structure within stocks

If substructuring of the five currently managed stocks of herring in British Columbia is present, then genetic differences among putative populations within stocks must be larger than annual variation within populations. This implies that there is a high degree of homing to the spawning location, and that genetic differences or genetic signal are greater than annual variation or sampling noise. Gene diversity analysis was used to determine the magnitudes of variation among samples within putative populations and among putative populations within stocks for herring in British Columbia. For herring along the east coast of the Queen Charlotte Islands, significant population differentiation was observed when herring spawning in Skidegate Inlet, Selwyn Inlet, Section Cove, and Skincuttle Inlet were compared, with the differentiation largely observed at Cpa27 (Table 3). Allele frequencies of Skidegate Inlet herring at Cpa27 were significantly different when compared with herring spawning at more southern locations along the east coast of the Queen Charlotte Islands and at somewhat earlier times ($P<0.05$). As Skidegate Inlet is outside of the current management area for this stock, comparisons were conducted among herring spawning in Selwyn Inlet, Section Cove, and Skincuttle Inlet. No differentiation was observed at any of the 15 loci surveyed. Variation was, on average, greater among sample years within populations than among the three putative populations (Table 3). There is no evidence that herring spawning in Selwyn Inlet, Section Cove, or Skincuttle Inlet constitute a genetically distinct population in any of these three locations. Accordingly, all samples from these locations were pooled, and compared with herring spawning in Haswell Bay, where only a single sample was available, precluding it from inclusion in the gene diversity analysis as there was no measure of within population variation. No differentiation was observed between the pooled Selwyn/Section Cove/Skincuttle samples and the Haswell Bay sample (Table 4). There is no evidence of genetic substructure in herring within the management zone along east coast of the Queen Charlotte Islands.

In the Strait of Georgia, spawning is concentrated along the east coast of Vancouver Island, with minor spawning in the eastern Strait of Georgia along the mainland coast of British Columbia. Unlike the Queen Charlotte Islands, where samples were collected from the same inlet over time, most samples from the Strait of Geogia have only been collected from one specific location in one year (Table 1). However, the geographic proximity of many of the samples was quite close, and thus should have sampled the same population, if it exists. In order to minimize the geographic spread of samples from a putative population, gene diversity analysis was restricted to samples along the east coast of Vancouver Island. Three putative populations

were evaluated, with geographic locations adjacent to Denman and Hornby Islands, Parksville, and Nanaimo. The gene diversity analysis indicated that over 99.8% of the variation occurred within populations, with no differentiation observed at any locus (Table 5). Indeed, on average, there was no variation at all attributable to population differentiation. There is no evidence of genetic substructure in herring along the east coast of Vancouver Island between Denman and Hornby Islands and Nanaimo. These samples were pooled and considered as a single population and compared with single samples from Bargain Harbour and Secret Cove along the mainland coast. No differentiation was observed between the east coast of Vancouver Island population and the Bargain Harbour sample, but significant differentiation was observed at five of the 15 loci surveyed between the Vancouver Island population and the Secret Cove sample (Table 4). However, as only a single sample was available from the Secret Cove location, it was not possible to evaluate whether this differentiation is stable over time. It is not possible to evaluate whether the differentiation is due to sampling error or population genetic differentiation. Significant differentiation at 10 of 15 loci was also observed between the Vancouver Island population and herring from Portage Inlet in Victoria harbour, as well as at eight loci between the Vancouver Island population and herring from Cherry Point in Washington (Table 4). Significant differentiation at 12 loci was also observed between the Cherry Point sample and the Portage Inlet sample, the geographically closest Canadian sampling site. Herring in Victoria harbour and Cherry Point may be distinct from the Vancouver Island population, but further samples are required to evaluate whether this differentiation is stable over time.

Four putative populations were considered for the west coast of Vancouver Island herring stock, with the populations defined by inlets or sounds along the coast in the management area. The gene diversity analysis indicated that about 99.6% of the variation occurred within populations, with no differentiation observed at any locus (Table 6). On average, there was no variation at all attributable to population differentiation. These samples were pooled and considered as a single population and compared with single samples from Klaskish Inlet and Winter Harbour along the northwest coast of Vancouver Island. No differentiation was observed between the west coast of Vancouver Island population and the Klaskish Inlet sample, but significant differentiation was observed at two of the 15 loci surveyed between the Vancouver Island population and the Winter Harbour sample (Table 4). The Winter Harbour sample is derived from the most northerly location on the west coast of Vancouver Island, so it is possible that there may be a local population, but additional sampling will be required to confirm that a genetically discrete population spawns in Winter Harbour.

Two putative populations were considered for the North Coast herring stock, with the two populations about 60 km apart. The gene diversity analysis indicated that about 99.9% of the variation occurred within populations, with no differentiation observed at any locus between the two putative populations (Table 7). None of the observed variation was attributable to population differentiation. There is no evidence to indicate the existence of genetically discrete spawning populations within the North Coast herring stock.

Four putative populations were considered for the Central Coast herring stock, with the two most distal populations about 120 km apart. As with the North Coast stock, about 99.9% of the variation occurred within populations, with no differentiation observed among the four putative populations (Table 8). Annual variation within populations was greater than any differentiation among putative populations. There is no evidence to indicate the existence of genetically discrete spawning populations within the Central Coast herring stock.

Although herring spawning in Johnstone Strait are not considered as a stock for management purposes, population structure within this putative stock was also examined. With four putative

populations defined, no differentiation was observed among the four populations, with 99.6% of the variation observed within populations. Annual variation within populations was larger than any differences between putative populations, and thus there was no evidence to indicate the existence of genetically discrete spawning populations.

Structure among stocks

Given the lack of population structure within the five major stocks of herring that are currently managed and assessed in British Columbia, all samples within years within each stock were pooled, with the Skidegate Inlet, Secret Cove, Portage Inlet, and Winter Harbour samples excluded from the appropriate regional stocks. As population structure within stocks was very limited, we evaluated the level of differentiation among stocks, including Johnstone Strait as a sixth stock in the analysis. Very little genetic differentiation was observed among the six stocks of herring in British Columbia, as 99.9% of variation occurred within stocks. Greater differentiation occurred among sampling years within stocks than among stocks (Table 9), providing no evidence for genetic discreteness of these six stocks in British Columbia. This lack of regional structure is further illustrated in Fig. 1, as samples from specific stocks did not generally cluster together as a group, but were instead distributed among stocks. The Portage Inlet sample contained the most distinctive herring sampled in our survey.

Comparisons were possible between herring spawning in northern British Columbia and southeast Alaska. Five samples were used to characterize herring from southeast Alaska, along with five for the North Coast, four for the west coast of the Queen Charlotte Islands, and five for the east coast of the Queen Charlotte Islands (Skidegate Inlet samples not considered) (Table 1). Gene diversity analysis indicated that there was significant differentiation between west coast of Queen Charlotte Islands herring and those in southeast Alaska at Cha63 ($F_{1,7}$=12.09, P<0.05), and approached significance at Cpa6 (P<0.10). East coast of Queen Charlotte Islands herring were moderately differentiated from those in southeast Alaska at Cpa107 and Cpa115 (both P<0.10). On average, greater differentiation was observed between herring in southeast Alaska and those in the Queen Charlotte Islands compared with annual variation within each region, but the differentiation was weak. For the North Coast and southeast Alaska comparison, genetic differentiation approached significance at Cpa6, Cpa107, and Cpa115 (P<0.10), but on average, within region variation was larger than between region differences.

Discussion

High levels of genetic diversity were observed in the Pacific herring samples surveyed in our study, with an observed average heterozygosity over 15 loci of 0.85, very similar to other microsatellite loci surveyed in Pacific herring by O'Connell et al. (1998), and comparable to microsatellite variation in Atlantic herring (*C. harengus*) (Shaw et al. 1999). There was no reduction in heterozygosity at any sampling site that would indicate a recent population bottleneck. Although population sizes of herring in British Columbia declined to low levels during the 1960s (Hourston 1980), the declines in population size were not extensive enough to have reduced heterozygosity or the number of alleles at a locus substantially.

Virtually no population structuring was observed within the five currently managed stocks of herring in British Columbia, with 99.6-99.9% of the variation contained within samples, with virtually none of the variation distributed among putative populations within stocks. There is no evidence for genetically discrete populations of herring spawning in different bays or even inlets

within local stocks or management groupings. In particular, on the east coast of the Queen Charlotte Islands, there is no evidence of genetic differentiation among herring spawning in Selwyn Inlet, Section Cove, and Skincuttle Inlet. In the Strait of Georgia, the only possible evidence of substructuring within this stock was that of the Secret Cove and Portage Inlet samples. However, until additional samples are analyzed from these two sites in order to confirm the genetic differentiation of herring spawning in these locations, it is premature to conclude that they constitute separate populations. The other locations where there either are or may be genetically distinct populations, Skidegate Inlet on the east Coast of the Queen Charlotte Islands, Winter Harbour on northwest Vancouver Island, and Cherry Point in Washington are not included in current boundaries for stock assessment and management.

In order for local population differentiation to occur, herring spawning in a particular area must home and be isolated from other spawning herring through differences in timing of spawning, or the location of spawning must be isolated from other spawning areas, or both may occur. Differences in timing of spawning may have led to some genetically discrete local populations of herring. Herring spawning in Skidegate Inlet spawn later than in other locations sampled in British Columbia and southeast Alaska (samples collected April 15-18, 1998; May 7, 1999), and this later timing of spawning has provided enough reproductive isolation for genetic differentiation to occur. Herring spawning at Secret Cove in the Strait of Georgia tend to spawn somewhat earlier than in other locations in the Strait (sample collected March 2, 1999), perhaps enough of an isolating mechanism to allow for genetic differentiation. Herring spawning at Cherry Point, Washington were sampled May 2, 2000, approximately two months after spawning typically begins in the Strait of Georgia. This difference in timing of spawning has likely led to the observed genetic differentiation between Strait of Georgia herring and those from Cherry Point. Geographic isolation may have also led to differentiation of local populations. Herring spawning in Esquimault Harbour at the extreme southern end of Vancouver Island move in to Portage Inlet (where the samples were collected) prior to and just after spawning. As there is a restricted distribution of spawning herring in this area, geographic isolation of the spawning population may have led to differentiation of a local population. Esquimault Harbour/Portage Inlet herring also spawn in late March, later than herring in most other locations in the Strait of Georgia, and thus both geographic isolation and differences in timing of spawning may be isolating mechanisms to maintain the distinctiveness of these populations. Winter Harbour is the most extreme northwest location on Vancouver Island from which samples were obtained, and geographic isolation may have led to the development of a local population in the area.

There was a lack of genetic differentiation among the five regional stocks of herring assessed and managed in British Columbia, and no differentiation was observed when Johnstone Strait herring were included in the analysis. Lack of differentiation between putative stocks can occur even if gene flow among stocks is restricted if the stocks have only recently diverged, and not enough time has passed since divergence to allow sufficient genetic drift to occur to lead to stock differentiation. Alternatively, significant gene flow among putative stocks can lead to homogenization of allele frequencies, even if the putative stocks have been separated for thousands of years. In British Columbia, tagging data has indicated that homing to management areas has been about 85% (Hourston 1982). Additional analyses of all tagged herring indicated that homing ranged from 53% of released tagged fish in Johnstone Strait to 97% of tagged fish released off the west coast of Vancouver Island (Hay et al. 1999). However, tagged fish released from one of six regions and that were at large for one year or longer were usually recovered in all other regions. These levels of gene flow, if the migrants are successful at reproducing, will lead to homogenization of allele frequencies, and is the most likely explanation for the lack of genetic differentiation among putative stocks of herring in British

Columbia. Although there was a lack of genetic differentiation among putative stocks of herring in British Columbia, all herring should not be considered as a single stock for assessment and management. There is straying among putative herring stocks, but the levels of straying may not be sufficient to offset overexploitation of herring in specific regions. Therefore, exploitation of herring should continue to be distributed geographically in British Columbia, in order to ensure maintenance of diversity that may not have been detected in our survey of microsatellite loci.

Genetic structuring of Alaskan herring populations has been reported by O'Connell et al. (1998), and for Atlantic herring in Norwegian waters and the Barents Sea by Shaw et al. (1999). Both studies were based on microsatellite surveys where only one year of samples was analyzed, and conclusions drawn on population structure without a measure of within population variation available. Subsequent sampling of the Alaskan putative populations indicated that temporal or annual variation was as large or larger than any differentiation between putative local populations, and thus characterization of separate populations in the Gulf of Alaska was not warranted (J. Olsen, Alaska Department of Fish & Game, Anchorage, pers. comm.). However, the difference between Bering Sea and Gulf of Alaska stocks was maintained over time. Demonstration that population differentiation is persistent over time increases the likelihood that the appropriate population structure has been elucidated (Waples 1998).

Divergent views have been expressed on population structure of Atlantic herring. In one case, discrete herring populations were thought to exist, with larval retention in the spawning area and general homing to the natal spawning area the mechanisms maintaining population distinctiveness (Iles and Sinclair 1982). Conversely, Smith and Jamieson (1986) suggested that herring populations fluctuate in size and the range occupied, and that straying among spawning populations do not result in distinct local populations. Alternatively, McQuinn (1997) suggested that there is a metapopulation structure in herring, with local population discreteness maintained by homing to initial spawning areas, not necessarily natal spawning areas, while new recruits to a population learn migration patterns and spawning areas from existing spawners within the population. Although genetically distinct local populations of herring exist in British Columbia, they are the exception, with differences in timing of spawning the main isolating mechanism. In these populations, discreteness is maintained by homing to natal spawning grounds, with a low rate of straying into the population, as there are few herring spawning in adjacent locations at the same time. For most herring in British Columbia, spawning is concentrated in March, and straying among spawning populations is substantial enough to prevent the development of genetically distinct populations in most areas.

Recommendations

1. As no population structure was observed in any of the five currently defined stocks (except for the Strait of Georgia), there is no genetic basis for management and assessment on a finer scale than is currently conducted.

2. In the Strait of Georgia, the possible distinctiveness of herring spawning at Secret Cove and Esquimault Harbour/Portage Inlet needs to be confirmed. If they are genetically distinct, the Strait of Georgia fishery should be conducted in a manner to conserve the diversity of these populations.

3. Although there was no consistent genetic differentiation among the five defined stocks of herring in British Columbia, prudent management action suggests that herring continue to

be assessed and managed on a five-stock basis. In particular, exploitation should be distributed over herring in all five regions as appropriate, and not concentrated on herring in a specific region.

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Table 1. Population sample, collection years, total number of fish analyzed, expected heterozygosity (H_e), and observed heterozygosity (H_o) for 65 samples of herring in nine regions in southeast Alaska, British Columbia, and Washington.

Population	Years	N	H_e	H_o
	Southeast Alaska			
North Sitka	2000	90	0.90	0.87
South Sitka	2000	94	0.89	0.88
Kirk Point	2000	96	0.88	0.88
Mary Island	2000	93	0.88	0.87
Seymour Canal	2000	166	0.88	0.87
	Queen Charlotte Islands - east coast			
Skidegate Inlet	1998, 1999	227	0.87	0.84
Selwyn Inlet	1998, 1999, 2000	397	0.88	0.86
Section Cove	1998, 1999	174	0.87	0.85
Skincuttle Inlet	1998, 1999, 2000	474	0.88	0.86
Haswell Bay	2000	150	0.88	0.89
Skaat Harbour	2000	164	0.88	0.86
	Queen Charlotte Islands - west coast			
Rennell Sound	1999	68	0.87	0.85
Port Louis	1999	73	0.88	0.84
Inskip Channel	1999	137	0.88	0.85
Peel Inlet	1999	92	0.87	0.83
	North Coast			
Big Bay	1999	143	0.87	0.84
Venn Passage	1999	147	0.88	0.84
Tree Bluff	2000	159	0.88	0.84
Gurd/Kitkatla	1999	165	0.88	0.85
Kitkatla	2000	161	0.87	0.87
	Central Coast			
Spiller Channel	1997, 1999, 2000	308	0.87	0.84
Powell Anchorage	1999	69	0.88	0.85
Dundivan Inlet	1999	260	0.88	0.85
Gale Passage	2000	175	0.88	0.89
Illahie Inlet	1999	122	0.88	0.83

Pruth Anchorage	1999	146	0.86	0.84
East Higgins	2000	192	0.88	0.83
Kitasu Bay	2000	172	0.88	0.87
Smith Inlet	2000	159	0.88	0.88
Stryker Bay	1999	117	0.88	0.85
Takush Harbour	1999	129	0.88	0.86
	Johnstone Strait			
Beaver Harbour	1999	145	0.88	0.84
Hardy Bay	2000	172	0.89	0.83
Wakeman Sound	1999	10	0.89	0.83
Thompson Sound	1997, 1999	179	0.89	0.84
Loughborough Inlet	1997, 1999	147	0.89	0.82
Bute Inlet	1999	358	0.89	0.87
	Strait of Georgia			
Longbeak Point	1997	95	0.88	0.86
Henry Bay	1999	150	0.88	0.84
Norman Point	1999	118	0.88	0.85
Whalebone Point	1999	261	0.88	0.84
Bowser	1999	260	0.88	0.86
Chrome Island	2000	137	0.86	0.84
Komas Bluff	2000	171	0.87	0.86
Fanny Bay	2000	66	0.84	0.87
French Creek	1999	236	0.88	0.84
Parksville Bay	2000	127	0.87	0.86
Hammond Bay	2000	149	0.87	0.87
Jessie Island	1999	164	0.88	0.86
Link Island	1999	166	0.88	0.84
Portage Inlet	1999	97	0.86	0.82
Bargain Harbour	1999	125	0.88	0.85
Secret Cove	1999	175	0.87	0.85
	Vancouver Island – west coast			
Winter Harbour	1999	135	0.88	0.84
Klashish Inlet	1999	131	0.87	0.84

Nootka Sound	1999, 2000	312	0.88	0.86
McKay	1999	94	0.88	0.85
Hesquiat Harbour	1999	65	0.88	0.85
Syndey Inlet	1999, 2000	366	0.88	0.86
Esperanza Inlet	1999, 2000	331	0.89	0.87
Spilling Island	1997	154	0.88	0.82
Castle Rock	1999	136	0.87	0.83
Bryant Island	1999	151	0.88	0.84
Forbes	2000	161	0.87	0.85
	Washington			
Cherry Point	2000	164	0.90	0.86

Table 2. Number of alleles, expected heterozygosity (H_e), observed heterozygosity (H_o), percent significant Hardy-Weinberg equilibrium tests (HWE, N=65 tests), and F_{ST} (standard deviation in parentheses) among 65 herring samples for 15 microsatellite loci.

Locus	Alleles	H_e	H_o	HWE	F_{ST}
Cpa4	24	0.91	0.88	4.6	0.0016 (0.0005)
Cpa6	29	0.71	0.68	9.2	0.0023 (0.0005)
Cpa8	38	0.92	0.85	11.5	0.0047 (0.0007)
Cpa27	26	0.74	0.72	1.5	0.0074 (0.0030)
Cha63	35	0.90	0.89	1.5	0.0015 (0.0005)
Cpa100	47	0.94	0.91	6.1	0.0010 (0.0003)
Cpa103	30	0.89	0.86	1.5	0.0005 (0.0003)
Cpa104	63	0.96	0.97	3.1	0.0009 (0.0004)
Cpa107	33	0.88	0.87	3.1	0.0049 (0.0004)
Cpa107a	42	0.83	0.78	9.2	0.0041 (0.0011)
Cha113	36	0.87	0.86	3.1	0.0009 (0.0005)
Cpa114	31	0.89	0.86	3.1	0.0014 (0.0006)
Cpa115	47	0.91	0.85	52.3	0.0035 (0.0008)
Cpa125	50	0.94	0.94	4.6	0.0009 (0.0004)
Cpa134	57	0.91	0.89	4.6	0.0005 (0.0002)
All loci	39	0.88	0.85		0.0023 (0.0005)

Table 3. Hierarchical gene-diversity analysis of four putative populations of herring along the east coast of the Queen Charlotte Islands: Skidegate Inlet (sampled in 1998, 1999), Selwyn Inlet (1998,1999,2000), Section Cove (1998, 1999, Skaat Harbour 2000), and Skincuttle Inlet (1998, 1999, 2000) for 15 microsatellite loci. The relative diversity owing to sampling years within populations and among populations is indicated.

Locus	With Skidegate Inlet			Without Skidegate Inlet		
	Within pops	Among years within pops	Among pops	Within pops	Among years within pops	Among pops
Cpa4	0.9990	0.0010	0.0000	0.9986	0.0014	0.0000
Cpa6	0.9977	0.0000	0.0023*	0.9982	0.0000	0.0018
Cpa8	0.9980	0.0020	0.0000	0.9980	0.0020	0.0000
Cpa27	0.9841	0.0000	0.0159**	0.9999	0.0000	0.0001
Cha63	0.9994	0.0000	0.0006	0.9996	0.0000	0.0004
Cpa100	0.9997	0.0000	0.0003	0.9996	0.0000	0.0004
Cpa103	0.9995	0.0005	0.0000	0.9993	0.0006	0.0000
Cpa104	0.9991	0.0002	0.0007	0.9997	0.0003	0.0000
Cpa107	0.9951	0.0017	0.0032	0.9993	0.0007	0.0000
Cpa107a	0.9984	0.0011	0.0005	0.9990	0.0008	0.0002
Cha113	0.9990	0.0000	0.0010	0.9987	0.0000	0.0013
Cpa114	0.9988	0.0012	0.0000	0.9999	0.0001	0.0000
Cpa115	0.9960	0.0019	0.0021	0.9978	0.0022	0.0000
Cpa125	0.9998	0.0000	0.0002	0.9999	0.0000	0.0001
Cpa134	0.9997	0.0003	0.0000	0.9993	0.0007	0.0000
All	0.9981	0.0005	0.0014	0.9995	0.0004	0.0001

* indicates $0.10 < P < 0.05$.

** indicates $P < 0.05$.

Table 4. Probability of homogeneity of allele frequencies estimated from pairwise probability tests derived from GENEPOP version 3.1 with the Markov-Cpain approach using χ^2 probability values (Raymond and Rousset 1995). Values considered statistically significant are in bold type. Sample comparisons are:

1) Haswell Bay versus combined Selwyn, Skincuttle, Section Cove, and Skaat Harbour
2) Portage Inlet versus combined east coast Vancouver Island (ECVI) samples (13 locations)
3) Secret Cove versus combined ECVI samples (13 locations)
4) Bargain Harbour versus combined ECVI samples (13 locations)
5) Cherry Point versus combined ECVI samples (13 locations)
6) Cherry Point versus Portage Inlet
7) Winter Harbour versus pooled WCVI samples (12 location/year combinations)
8) Klaskish Inlet versus pooled WCVI samples (12 location/year combinations)

	Sample Comparison							
Locus	1	2	3	4	5	6	7	8
Cpa4	0.2049	**0.0000**	0.1492	0.7359	0.4292	**0.0000**	0.5479	0.9321
Cpa6	0.4703	**0.0000**	0.0329	0.8092	**0.0038**	**0.0006**	0.0438	0.3874
Cpa8	0.0890	0.0164	0.4208	0.0062	0.0089	**0.0000**	0.1033	0.4283
Cpa27	0.6317	**0.0000**	**0.0000**	0.9393	**0.0002**	**0.0000**	0.0482	0.2752
Cha63	0.6972	0.0952	0.4996	0.9266	0.6615	0.0419	0.2551	0.1853
Cpa100	0.4397	**0.0000**	0.0535	0.5598	0.0468	**0.0008**	0.3178	0.3108
Cpa103	0.4927	0.4037	0.6599	0.1965	0.0432	0.0443	0.7188	0.7269
Cpa104	0.2967	**0.0000**	0.0089	0.8867	**0.0000**	**0.0000**	0.3900	0.3689
Cpa107	0.0685	**0.0000**	**0.0000**	0.5042	**0.0000**	**0.0000**	**0.0019**	0.7024
Cpa107a	0.7224	**0.0000**	**0.0030**	0.4787	**0.0000**	**0.0053**	0.3174	0.6796
Cha113	0.2524	0.0152	0.3307	0.1597	0.7279	**0.0037**	0.9163	0.7298
Cpa114	0.4617	**0.0000**	0.2142	0.1152	**0.0024**	**0.0044**	**0.0033**	0.2355
Cpa115	0.3352	**0.0000**	**0.0000**	0.1395	**0.0000**	**0.0000**	0.9535	0.9732
Cpa125	0.9279	**0.0000**	**0.0000**	0.9974	**0.0001**	**0.0024**	0.7752	0.1485
Cpa134	0.1332	0.4808	0.7347	0.3160	0.0967	0.1279	0.7092	0.5314

Table 5. Hierarchical gene-diversity analysis of three putative populations of herring along the east coast of Vancouver Island: Population 1 (Longbeak Point 1997, Henry Bay 1999, Norman Point 1999, Whalebone Point 1999, Bowser 1999, Chrome Island 2000, Komas Bluff 2000, Fanny Bay 2000), Population 2 (French Creek 1999, Parksville Bay 2000), and Population 3 (Jessie Island 1999, Link Island 1999, Hammond Bay 2000) for 15 microsatellite loci. The relative diversity owing to sampling years within populations and among populations is indicated.

	Absolute diversity		Relative diversity		
Locus	Total	Within Populations	Within Populations	Among years within pops	Among pops
Cpa4	0.9056	0.9030	0.9971	0.0029	0.0000
Cpa6	0.6817	0.6807	0.9985	0.0015	0.0000
Cpa8	0.9117	0.9063	0.9941	0.0059	0.0000
Cpa27	0.7303	0.7301	0.9997	0.0003	0.0000
Cha63	0.8991	0.8988	0.9997	0.0003	0.0000
Cpa100	0.9435	0.9434	0.9999	0.0000	0.0001
Cpa103	0.8863	0.8839	0.9973	0.0027	0.0000
Cpa104	0.9559	0.8636	0.9997	0.0003	0.0000
Cpa107	0.8786	0.8783	0.9985	0.0015	0.0000
Cpa107a	0.8169	0.8135	0.9958	0.0042	0.0000
Cha113	0.8655	0.8646	0.9990	0.0010	0.0000
Cpa114	0.8864	0.8815	0.9945	0.0055	0.0000
Cpa115	0.9126	0.9118	0.9991	0.0009	0.0000
Cpa125	0.9428	0.9423	0.9995	0.0004	0.0001
Cpa134	0.9153	0.9144	0.9990	0.0010	0.0000
All			0.9981	0.0019	0.0000

Table 6. Hierarchical gene-diversity analysis of four putative populations of herring along the west coast of Vancouver Island: Population 1 (Spilling Islet 1997, Castle Rock 1999, Bryant Islands 1999, Forbes Island 2000), Population 2 (Sydney Inlet 1999, 2000), Population 3 (Nootka Sound 1999, 2000, McKay Pass 1999, Hesquiat Harbour 1999), and Population 4 (Esperanza Inlet 1999, 2000) for 15 microsatellite loci. The relative diversity owing to sampling years within populations and among populations is indicated.

	Absolute diversity		Relative diversity		
Locus	Total	Within Populations	Within Populations	Among years within pops	Among pops
Cpa4	0.9122	0.9078	0.9952	0.0012	0.0036
Cpa6	0.7552	0.7264	0.9619	0.0381	0.0000
Cpa8	0.8821	0.8611	0.9762	0.0215	0.0023
Cpa27	0.7541	0.7156	0.9489	0.0511	0.0000
Cha63	0.8691	0.8422	0.9690	0.0310	0.0000
Cpa100	0.9244	0.9157	0.9906	0.0094	0.0000
Cpa103	0.8820	0.8637	0.9793	0.0177	0.0030
Cpa104	0.9338	0.9247	0.9923	0.0097	0.0000
Cpa107	0.8738	0.8606	0.9849	0.0095	0.0056
Cpa107a	0.8346	0.8154	0.9770	0.0210	0.0020
Cha113	0.8609	0.8413	0.9772	0.0228	0.0000
Cpa114	0.8840	0.8654	0.9790	0.0192	0.0018
Cpa115	0.7390	0.7056	0.9548	0.0452	0.0000
Cpa125	0.8894	0.8549	0.9612	0.0388	0.0000
Cpa134	0.9064	0.8986	0.9914	0.0086	0.0000
All			0.9959	0.0221	0.0000

Table 7. Hierarchical gene-diversity analysis of two putative populations of herring along the north coast of British Columbia: Population 1 (Big Bay 1999, Venn Passage 1999, Tree Bluff 2000) and Population 2 (Gurd Island 1999, Kitkatla Channel 2000) for 15 microsatellite loci. The relative diversity owing to sampling years within populations and among populations is indicated.

	Absolute diversity		Relative diversity		
Locus	Total	Within Populations	Within Populations	Among years within pops	Among pops
Cpa4	0.9049	0.9034	0.9983	0.0004	0.0013
Cpa6	0.7037	0.7032	0.9993	0.0007	0.0000
Cpa8	0.9191	0.9184	0.9992	0.0008	0.0000
Cpa27	0.7250	0.7243	0.9990	0.0010	0.0000
Cha63	0.8919	0.8865	0.9939	0.0061	0.0000
Cpa100	0.9436	0.9420	0.9983	0.0004	0.0013
Cpa103	0.8776	0.8761	0.9983	0.0017	0.0000
Cpa104	0.9597	0.9596	0.9999	0.0000	0.0001
Cpa107	0.8755	0.8755	1.0000	0.0000	0.0000
Cpa107a	0.8427	0.8405	0.9974	0.0026	0.0000
Cha113	0.8629	0.8622	0.9992	0.0001	0.0007
Cpa114	0.8838	0.8825	0.9985	0.0015	0.0000
Cpa115	0.9072	0.9062	0.9989	0.0011	0.0000
Cpa125	0.9487	0.9474	0.9986	0.0014	0.0000
Cpa134	0.9084	0.9073	0.9988	0.0012	0.0000
All			0.9987	0.0013	0.0000

Table 8. Hierarchical gene-diversity analysis of four putative populations of herring along the central coast of British Columbia: Population 1 (East Higgins 2000, Kitasu Bay 2000), Population 2 (Spiller Channel 1997, 1999, 2000, Powell Anchorage 1999, Dundivan Inlet 1999, Stryker Bay 1999, Gale Passage 2000), Population 3 (Illahie Inlet 1999, Pruth Anchorage 1999), and Population 4 (Takush Harbour 1999, Smith Inlet 2000) for 15 microsatellite loci. The relative diversity owing to sampling years within populations and among populations is indicated.

	Absolute diversity		Relative diversity		
Locus	Total	Within Populations	Within Populations	Among years within pops	Among pops
Cpa4	0.9072	0.9057	0.9984	0.0013	0.0003
Cpa6	0.6951	0.6931	0.9971	0.0029	0.0000
Cpa8	0.9134	0.9098	0.9961	0.0039	0.0000
Cpa27	0.7754	0.7743	0.9986	0.0004	0.0010
Cha63	0.8937	0.8926	0.9988	0.0012	0.0000
Cpa100	0.9442	0.9434	0.9992	0.0008	0.0000
Cpa103	0.8858	0.8850	0.9991	0.0008	0.0001
Cpa104	0.9583	0.9579	0.9996	0.0001	0.0003
Cpa107	0.8795	0.8790	0.9994	0.0001	0.0004
Cpa107a	0.8173	0.8141	0.9961	0.0039	0.0000
Cha113	0.8726	0.8725	0.9999	0.0001	0.0000
Cpa114	0.8896	0.8873	0.9974	0.0020	0.0006
Cpa115	0.9125	0.9100	0.9973	0.0015	0.0012
Cpa125	0.9442	0.9440	0.9998	0.0002	0.0000
Cpa134	0.9125	0.9122	0.9997	0.0003	0.0000
All			0.9985	0.0013	0.0002

Table 9. Hierarchical gene-diversity analysis of six putative stocks of herring in British Columbia: Stock 1 (East Coast Queen Charlotte Islands 1998, 1999, 2000), Stock 2 (North Coast 1999, 2000), Stock 3 (Central Coast 1997, 1999, 2000), Stock 4 (Strait of Georgia 1997, 1999, 2000), Stock 5 (West Coast Vancouver Island 1997, 1999, 2000), and Stock 6 (Johnstone Stait 1997, 1999, 2000) for 15 microsatellite loci. The relative diversity owing to sampling years within stocks and among stocks is indicated.

	Absolute diversity		Relative diversity		
Locus	Total	Within stocks	Within stocks	Among years within stocks	Among stocks
Cpa4	0.9081	0.9076	0.9994	0.0006	0.0000
Cpa6	0.7061	0.7053	0.9989	0.0008	0.0003
Cpa8	0.9173	0.9157	0.9983	0.0017	0.0000
Cpa27	0.7440	0.7424	0.9978	0.0002	0.0020
Cha63	0.8983	0.8979	0.9996	0.0003	0.0001
Cpa100	0.9442	0.9439	0.9997	0.0003	0.0000
Cpa103	0.8871	0.8850	0.9991	0.0008	0.0001
Cpa104	0.9575	0.9572	0.9997	0.0003	0.0000
Cpa107	0.8805	0.8800	0.9994	0.0002	0.0004
Cpa107a	0.8269	0.8253	0.9981	0.0013	0.0006
Cha113	0.8718	0.8711	0.9992	0.0008	0.0000
Cpa114	0.8907	0.8901	0.9993	0.0007	0.0000
Cpa115	0.9128	0.9116	0.9987	0.0011	0.0002
Cpa125	0.9451	0.9448	0.9997	0.0002	0.0001
Cpa134	0.9123	0.9122	0.9999	0.0001	0.0000
All			0.9993	0.0006	0.0001

Figure 1. Neighbor-joining dendrogram based on Cavalli-Sforza and Edwards (1967) chord distance for 65 herring samples from southeast Alaska, British Columbia, and Washington.